

Does the global microbiota consist of a few cosmopolitan species?

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[Keywords: cosmopolitanisms, endemics, microbes]

[Palabras clave: cosmopolitanismo, endémicos, microbios]

Biogeography studies the distribution of biodiversity over space and time. Currently, there is a strong debate on the biodiversity and biogeography of free-living microorganisms. For several years, morphological studies have promoted the idea that, at the global level, there is a relatively small number of cosmopolitan microbial species (Baas-Becking 1934; Finlay 2002, 2004; Fenchel 2005). This view has been the most popular until recently, when molecular data started to unveil a much more complex scenario. Within the realm of this controversy, the objectives of this work are twofold: a) to review the traditional viewpoints on microbial biodiversity and biogeography and, b) to present and discuss new molecular data which are challenging previous ideas.

Since the number of species relies on the chosen species definition, any discussion on biodiversity and biogeography needs to mention upon which species concept conclusions are based. So far, the Morphological Species Concept (MSC; species are groups of morphologically identical or very similar organisms (Futuyma 1998)) has been the most popular definition in studies on microbial biodiversity and biogeography. In a few cases, the Biological Species Concept (BSC; species are groups of interbreeding natural populations that are reproductively isolated from other such groups (Mayr 1942)) has been applied to microeuka-

ryotes where sexual reproduction is known (Andersen 1998). In a more controversial approach, a group of researchers working on prokaryotes have defined that organisms having more than 70% of DNA-DNA similarity belong to the same species (Wayne et al. 1987).

For years, the use of the MSC in microbial taxonomy has promoted the view that the global microbiota consists of a relatively small number of cosmopolitan species; '*the cosmopolitan view*' (Finlay 2002, 2004). The most popular hypothesis for explaining this putative pattern claims that due to their small sizes and huge abundances, microbes have no geographical barriers for their dispersal (Fenchel 2005). As a consequence, there is little opportunity for genetic diversification and therefore, a low number of cosmopolitan species should be expected. In agreement with these ideas, Griffin et al. (2002) indicate that between 10^{18} and 10^{20} microorganisms are transported annually through the atmosphere, making it difficult to imagine how topographic features of the Earth's surface could act as barriers for their dispersal. Morphological studies support the '*cosmopolitan hypothesis*' by indicating that there would be less than 5.000 species of microbes, a number quite low in comparison with the estimated 750.000 species of insects or 280.000 of all other animals (Papke & Ward 2004).

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Recibido: 20 de octubre de 2004; Fin de arbitraje: 16 de mayo de 2006; Aceptado: 16 de mayo de 2006

A lack of biogeographic patterns and a low global diversity for free-living microbes has been the most accepted view until the advent of molecular studies. Interestingly, some molecular data support the 'cosmopolitan hypothesis' by showing a low genetic differentiation between populations separated by continental distances (e.g. Darling et al. 2000; Montresor et al. 2003a). However, there are mounting data revealing a very different picture, as it will be described and discussed in the following sections.

Is there a relatively low number of microbial species?

The technical limitations during the times of the early taxonomists were probably an important factor in generating a false impression of a low number of microbial species. For instance, before the arrival of the electron microscope there were 12 algal classes, while today more than 30 are recognized (Andersen 1998). Although more advanced microscopes have contributed significantly to improve our knowledge, they still have a limit of resolution. This limit is not only technological: it is widely recognized that there are different microbial species and/or genetically isolated strains that are virtually indistinguishable using morphological characters (cryptic species/strains).

It has been proposed that cryptic species/strains are the product of natural selection exerting an important stabilizing force on particular morphologies that represent adaptive peaks (Potter et al. 1997; Finlay 2004). However, selection could be disruptive or absent on other areas of the genome. Thus, it would not be surprising if it is revealed that several well established microbial species defined on a morphological basis (morphospecies) are actually an agglomeration of a range of genetic and physiological strains/species that are morphologically undistinguishable. An increasing number of molecular studies are clearly pointing in this direction (e.g. Pace 1997; Potter et al. 1997; Daugbjerg et al. 2000; Coleman 1996, 2001a, 2001b; Casamatta et al. 2003; Kim et al. 2004; Wilson et al. 2005). Altogether, they are showing that several morpho-

species are in fact composed of genetically divergent populations or cryptic species. For instance, Montresor et al. (2003b) carried out morphological and genetic studies on different populations of the cosmopolitan marine dinoflagellate *Scrippsiella trochoidea* and found that within the same morphotype, there are strains which show a genetic differentiation that is in the order of what is normally found between other dinoflagellate species. In the light of their data, it seems likely that the morphotype known as *Scrippsiella trochoidea* is actually a complex of cryptic species.

A good example of how similar morphologies can mask biodiversity comes from coccoid picoplanktonic algae, which are mere tiny (<5 µm) balls that are present in most oceans. According to Potter et al. (1997), the morphology of these microeukaryotes provides so little information that it is not possible to go lower than the taxonomical 'Class' level. Moreover, sexual reproduction was rarely observed, so the BSC could not be used to ascertain their species status. In order to investigate the biodiversity of these picoplankters, Potter et al. (1997) carried out genetic studies on the 'brown-type tiny balls', which were morphologically indistinguishable between each other. Interestingly, they found that, lumped together as 'brown tiny balls', there are members of three distinct eukaryotic groups: the heterokont, the haptophyte and the green algae.

Another factor that may have contributed to an underestimation of the number of microbial species is that most studies have been carried out on cultivable organisms. Today it is estimated that > 99 % of microorganisms are not cultivable using standard techniques (Aman et al. 1995; Oren 2004). During the last decade, phylogenetic data from ribosomal DNA (rDNA) sequences directly amplified from environmental samples (environmental DNA surveys), revealed an unexpected diversity of prokaryotes (Giovannoni et al. 1990; Fuhrman et al. 1992; Hugenholtz et al. 1998). More recently, the same approach was used on marine microeukaryotes, revealing not only an unsuspected high diversity, but also the presence of several novel organisms with unknown close relatives (López-García et al.

2001; Moreira & López-García 2002). For instance, Moon-van der Staay et al. (2001) used the environmental DNA approach to investigate the eukaryotic diversity in marine picoplankton. They took one plankton sample (<3 µm) at a depth of 75 m in the equatorial Pacific Ocean and sequenced the small-subunit (SSU) rDNAs present in the whole sample. They obtained 35 SSU rDNA sequences, most of which belong to previously unknown members of the phyla prasinophytes, haptophytes, dinoflagellates, stramenopiles, choanoflagellates and acantharians. Moreover, six sequences were forming a clade that cannot be assigned to any known eukaryotic taxonomic group. In another study, Dawson and Pace (2002) used the environmental DNA approach for investigating the microeukaryotic biodiversity in anoxic sediments. By sequencing the SSU rDNA from marine and lake samples, they detected many previously unrecognized eukaryotes, including representatives of seven lineages that are not related to any known organism. Using the 'whole-genome shotgun sequencing' technique to microbial plankton from the Sargasso Sea, Venter et al. (2004) found an unexpected high diversity of oceanic prokaryotes and microeukaryotes.

Considering these results, it becomes apparent that the hypothesis proposing a low global diversity for microbes does not agree with nature. Thus, assuming that the real microbial diversity is much higher than previously recognized, the next natural step is to investigate if there are patterns in the distribution of that diversity.

Are microbial species cosmopolitan?

The 'cosmopolitan hypothesis' predicts that microbes will be present in all environments where they can live due to unrestricted dispersal capabilities. Despite some molecular data support this hypothesis (e.g. Darling et al. 2000; Montresor et al. 2003a), multiple lines of evidence indicate that there are microbial species/strains with restricted geographical distributions (Vincent 2000; Wilson et al. 2005; Martiny et al. 2006). For instance, Whitaker et al. (2003) showed that, on a global scale, popu-

lations of the hyperthermophilic prokaryote, *Sulfolobus*, are geographically isolated from one another. In other words, thousands of kilometers of separation have left a genetic imprint in *Sulfolobus*. Additionally, high levels of endemism were also found in soil bacteria (Fulthorpe et al. 1998) and in microbial eukaryotes. For example, in a study of testate amoeba, Wilkinson (2001) found that many species, with body sizes around 100 µm, are restricted either to the Arctic or the Antarctic. Several researchers indicate the existence of endemic lacustrine microalgae strains/species (Tyler 1996; Vincent 2000; Coleman 2001a; Casamatta et al. 2003; Taton et al. 2003; Wilson et al. 2005). Shayler and Siver (2004) mention the unique microalgal flora that is present in the Ocala National Forest (Florida, USA). Recent studies also show the existence of several genetically differentiated ecotypes within a marine planktonic cyanobacterium morphospecies (Coleman et al. 2006; Johnson et al. 2006).

Implications of new molecular data

Altogether, new molecular data indicate that: a) the diversity of free-living microbes is much higher than previously recognized and b) there are endemic as well as cosmopolitan species (e.g. Pace 1997; Fulthorpe et al. 1998; Glöckner et al. 2000; Massana et al. 2000; Sabbe et al. 2001, 2003; Wilkinson 2001; Taton et al. 2003; Whitaker et al. 2003; Oren 2004; Papke & Ward 2004; Martiny et al. 2006). This new knowledge has profound implications for the understanding of microbial diversification and biogeography. In particular, the discrepancy *per se* between molecular data and traditional concepts on the diversity and distribution of microbes, points to a very clear fact: we still know very little about the factors that promote the evolutionary diversification of microbes. The knowledge gained from approximately seven decades of evolutionary studies in macroorganisms is not enough to understand microbial diversification. This is due in large part to the fact that microbes normally differ from macroorganisms in having high dispersal, high reproductive rates and enormous individual abundances (Finlay 2002, 2004), all of which probably affect the tempo and mode of their evolution.

Geographical isolation has traditionally been regarded as the prevailing agent of microbial divergence (Papke & Ward 2004). However, molecular data suggest that local adaptation plays a significant role in microbial diversification (e.g. Rynearson & Armbrust 2000, 2004; Casamatta et al. 2003; Saez et al. 2003; Kim et al. 2004; Wilson et al. 2005; Coleman et al. 2006; Johnson et al. 2006). The role of natural selection in the divergence and eventual speciation of organisms in general has been recently reconsidered, receiving support from natural (Hendry et al. 2000; Rundle et al. 2000), laboratory (Rainey & Travisano 1998; Rainey et al. 2000) and theoretical (Doebeli et al. 2005) studies. In particular, there is increasing evidence that natural selection can generate exceptionally rapid divergences, as illustrated by the diverse macroorganisms that have colonized islands or lakes (Orr & Smith 1998; Coyne & Orr 2004). Evidence also indicates that natural selection can generate rapid divergences in microbes (Leblond et al. 2006; Logares et al. 2006).

Molecular data indicate that microbial dispersal can be restricted by distance and/or geographical features (e.g. Wilkinson 2001; Whitaker et al. 2003; Martiny et al. 2006). Following the classical speciation theory, dispersal restrictions will diminish gene flow between populations, which will then further diverge with time (by genetic drift and /or natural selection) to eventually form new strain/species. However, even if there were microbial species which had no geographical barriers for their dispersal, gene flow between their populations would not necessarily have to be high. Local adaptation of different populations to particular environmental conditions can constitute a considerable barrier to gene flow by lowering the fitness of immigrants from other populations (De Meester et al. 2002). Thus, high dispersal would be compatible with the emergence and permanence of genetically differentiated populations/strains and eventually endemic species. The most controversial new evidence indicates that microbial diversification can occur in the presence of gene flow (Rainey & Travisano 1998; Rainey et al. 2000; Friesen et al. 2004). The genetic mechanisms underlying this type of divergence are still poorly understood.

To date, molecular techniques have been highly successful in the investigation of microbial biodiversity and biogeography, but new studies including more taxa from different locations are needed to gain a better understanding of microbial diversification, biodiversity and biogeography. It should always be remembered that most of the diversity of life is microscopic, thus, studying microbial diversification is necessary for understanding the process of evolution as a whole. There are also practical reasons for investigating microbial diversity and biogeography. For instance, in the search for novel drugs or compounds of commercial importance as well as in the fight against microbial diseases (like malaria) and microbial species that produce enormous economical losses (e.g. dinoflagellates during blooms).

ACKNOWLEDGMENTS

Special thanks to K. Rengefors, L. A. Hansson (Lund University) and J. Leblond (Middle Tennessee State University) for providing valuable comments and suggestions that helped to improve this manuscript. The Swedish Research Council and the SEED project contract, GOCE-CT-2005-003875 (European Commission Directorate General Research), to K. R. provided financial support.

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